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BIOGEOGRAPHIC SIGNIFICANCE OF LOW-ELEVATION RECORDS FOR *NEOTOMA CINEREA* FROM THE NORTHERN BONNEVILLE BASIN, UTAH

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Abstract.—The existence of low-elevation populations of *Neotoma cinerea* in the northern Bonneville Basin shows either that these mammals can survive many thousands of years in xeric habitats or that they can move across xeric lowlands far more readily than has been appreciated, or both. Current models of Great Basin small mammal biogeography are far too static to encompass properly the interaction of the wide range of geographical and biological variability that has produced the modern distribution of those mammals that have, for several decades, been treated as "montane" within the Great Basin.

Key words: Great Basin, biogeography, island biogeography, Neotoma cinerea, *mammals.*

Ever since J. H. Brown's insightful analyses of Great Basin small mammal biogeography (Brown 1971, 1978, see also Lomolino et al. 1989), biogeographers have treated the bushy-tailed woodrat (*Neotoma cinerea*) as a member of an assemblage of small mammals that is currently isolated on Great Basin mountains. The composition of this assemblage is of particular importance because it has been used to generate and test hypotheses about the past and future of Great Basin "montane" mammals (e.g., Grayson 1987, 1993, Patterson 1990, Cutler 1991, McDonald and Brown 1992, Murphy and Weiss 1992, Grayson and Livingston 1993). However, there is a growing body of data that suggests that this group of mammals lacks the coherence that has been assigned to it. Here, we add to that growing body and call for a more dynamic view of Great Basin small mammal historic biogeography.

Neotoma cinerea on Homestead Knoll, Utah

Located a few km west and south of Great Salt Lake in north central Utah, the Lakeside Mountains are formed from a complex of north-trending hills, ridges, knolls, and small mountains (Fig. 1). The northwestern-most spur of this complex is Homestead Knoll, a low (maximum elevation 1615 m), rocky promontory that is devoid of active springs and permanent

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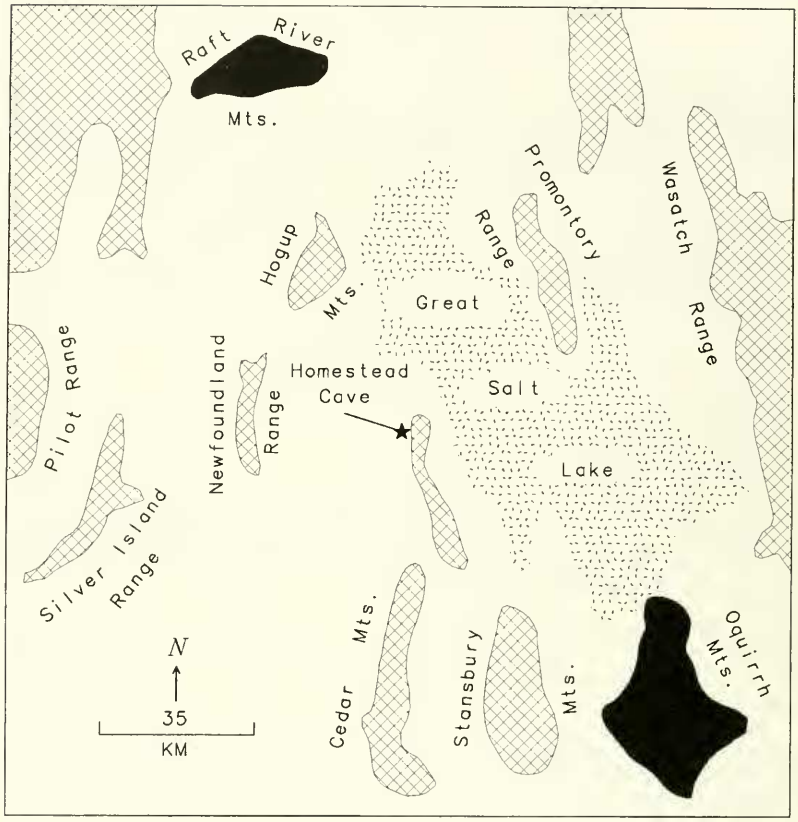

Fig. 1. Location of Homestead Cave within the northern Bonneville Basin.

streams, and that is separated from other parts of the Lakeside group by valleys whose maximum elevations do not exceed 1465 m.

The barren playa of Pleistocene Lake Bonneville is located to the immediate west and northwest of Homestead Knoll. Vegetation of the knoll is dominated by shrubs and grasses, although there are a few scattered Utah junipers (*Juniperus osteosperma*) on its highest reaches.

Most prominent among the shrubs are *Atriplex confertifolia*, *Tetradymia spinosa*, and *Tetradymia glabrata*. *Artemisia tridentata* is present along seasonally moist drainages, while *Artemisia spinescens*, *Chrysothamnus* sp., and *Sarcobatus vermiculatus* are present but uncommon above the flanks of the knoll. *Artemisia nova* occurs on those flanks as does *Ceratoides lanata*, while *S. vermiculatus* becomes increasingly abundant as the valley bottoms are approached. We made no attempt to identify the grasses that form the understory beneath the shrubs, but cheatgrass (*Bromus tectorum* and, perhaps, *B. rubens*) is extremely abundant on the flats beneath the knoll.

Homestead Knoll is dotted by a number of caves, one of which, Homestead Cave, sits on the northwestern edge of the knoll at an elevation of 1406 m (Fig. 2). Approximately 11 m wide and 6 m high at its mouth, this 25-m-deep cave has, since 1992, been the focus of interdisciplinary paleoecological work funded by the Department of Defense. With D. B. Madsen of the Utah Geological Survey, 3 authors of this paper (DKG, SDL, and MWS) have been involved with the excavation and analysis of a deep sequence of vertebrate remains from this site. To provide background data for the analysis of the mammalian component of the excavated fauna, we conducted a brief (270 trap-night) small mammal survey in the vicinity of Homestead Cave in June 1995.

With 1 exception, the results of this survey were quite predictable. Trapping success was low, with 3 species—*Dipodomys ordii* (3 individuals), *Peromyscus maniculatus* (11 individuals), and *Neotoma lepida* (6 individuals)—comprising nearly the entire trapped assemblage. The 1 exception, however, was remarkable: we

Fig. 2. Location of Homestead Cave (white arrow) on Homestead Knoll; the prominent terraces represent Provo, post-Provo regressive, and Stansbury beaches left by the waters of Pleistocene Lake Bonneville.

took a single *Neotoma cinerea* from the back of Homestead Cave itself.

Because this individual was live-trapped and released, we cannot report its age or sex or provide standard measurements. Even though we do not have a voucher specimen, we do have an excellent videotape of the animal (taken by MWS and on file at the Utah Geological Survey), and there is no doubt as to the identification of the individual.

Vegetation in the immediate vicinity of Homestead Cave departs from the Homestead Knoll vegetation that we have described in only 1 major way: the mouth of the cave supports a luxuriant growth of *Ribes cereum* immediately beneath the dripline. It would be surprising if this shrub were not heavily utilized by both *Neotoma cinerea*, taken at the rear of the cave, and *Neotoma lepida*, taken at the front.

OTHER LOW-ELEVATION NORTHERN BONNEVILLE BASIN RECORDS FOR *NEOTOMA CINEREA*

Our discovery of *Neotoma cinerea* on Homestead Knoll led us to search the mammal collection at the Utah Museum of Natural History, University of Utah, for additional records of this species from other low-elevation settings in the northern Bonneville Basin. We were quite successful in this search:

(a) **Locomotive Springs:** The only previously published low-elevation record for *Neotoma cinerea* for the northern Bonneville Basin was provided by Durrant (1952:348; UU 5048) as having been taken in October 1947 from "Statehouse, Locomotive Springs, 5500 ft. [1676 m]." However, we are unable to determine the location of "Statehouse" and are otherwise hesitant to accept this record because of the substantial difference between the actual elevation of Locomotive Springs (1283 m) and the reported elevation of "Statehouse" (1676 m). Given the well-watered nature of Locomotive Springs, the record might be accurate, but it is in need of verification. Locomotive Springs is approximately 60 km north of Homestead Knoll.

(b) **Lakeside Mountains:** An adult male *Neotoma cinerea* (UU 14374) was collected "5 mi. E Lakeside, 4600 ft. [1402 m]" in June 1957. This distance and direction from Lakeside, however, describe a point in the Great Salt Lake. If

the actual direction were southeast, the specimen could have come from Cave Ridge on the eastern edge of the Lakeside Mountains, approximately 10 km east of Homestead Knoll.

(c) **Newfoundland Mountains:** A series of three juvenile *Neotoma cinerea* (UU 9995, 9996, 9998) were collected in June 1951 from an unspecified site at the north end of the Newfoundland Mountains. The collector's field notes do not provide the elevation of the site but do indicate that the specimens came from an area of granite cliffs with a plant community that included *Juniperus* and *Tetradymia*. The north end of the Newfoundland Mountains is approximately 40 km west-northwest of Homestead Knoll.

(d) **Cedar Mountains:** There are records for *Neotoma cinerea* from 2 separate locations in the southern Cedar Mountains: 4 from the Cane Springs area (elevation 1768 m; UU 26340, 27297, 27299, and 27301-2, collected between October 1952 and January 1953), and 1 from the "south end Cedar Mtn., 4850 ft. [1478 m]." This last specimen is reported to have been caught in a garage, suggesting that it may have come from near Dugway. Although these specimens come from no closer than 95 km to the south of Homestead Cave, we mention them because they establish the likelihood that *Neotoma cinerea* occurs in suitable habitat throughout the Cedar Range.

Biogeographic Considerations

Although *Neotoma cinerea* has frequently been treated as being isolated on Great Basin mountains (Brown 1971, 1978, Grayson 1993), these records demonstrate that bushy-tailed woodrats can and do exist at low elevations in arid contexts within at least the northern Bonneville Basin. How, one must wonder, did *Neotoma cinerea* come to occupy such arid, low-elevation settings as the Newfoundland Mountains (maximum elevation 2130 m) and isolated knolls on the Lakeside Mountains (maximum elevation 2020 m)?

It is well established that during the late Pleistocene, bushy-tailed woodrats were far more widely distributed within the Great Basin than they are today, occupying low-elevation settings where they are no longer found (Grayson 1988, 1993). As a result, it is reasonable to speculate that these animals were also widespread in this part of the northern Bonneville Basin during those years. We can, however, do much more than speculate about the history of *N. cinerea* in the Homestead Knoll area.

With a maximum elevation of 1615 m, Homestead Knoll was covered by the waters of Pleistocene Lake Bonneville 14,500 years B.P., when Pleistocene Lake Bonneville was at its high (see Figure 2). Obviously, Homestead Knoll must have received its woodrats after this time, but when this occurred is not clear. Between 14,500 and at least 14,200 years B.P., when Lake Bonneville stood at the Provo level, Homestead Knoll was an island of approximately 770 acres. Not until Lake Bonneville fell to a local elevation of 1463 m did this island become connected to the main body of the Lakeside Mountains. Once this occurred, Homestead Knoll became part of the faunal mainland and would have been open to overland colonization by terrestrial mammals.

Unfortunately, we do not know when the lake fell to this level. However, we do have direct evidence from Homestead Cave concerning the regional history of *Neotoma cinerea*. Excavations in this cave have provided a rich, stratified sequence of vertebrate remains, the mammals of which are being identified and analyzed by one of the authors (DKG). To date, a substantial sample of mammal specimens from the 4 lowest Homestead Cave strata has been identified (37,381 specimens).

All 4 assemblages contain both *N. cinerea* and *N. lepida*, but the ratio of *N. cinerea* to *N. lepida* varies dramatically through time. In stratum I, which dates to between ca 11,300 and 10,000 years B.P., bushy-tailed woodrats make up 99.38% of the *Neotoma* fauna. In subsequent strata, however, they decline steadily in abundance; by stratum IV (ca 8200–7200 years B.P.), *N. cinerea* comprises only 4.74% of the *Neotoma* assemblage (Fig. 3). Similarly, *N. cinerea* contributes 23.97% of the total number of identified mammalian specimens in stratum I, a number that declines to 1.01% in stratum IV (Fig. 4).

The Homestead Cave fauna thus documents that *N. cinerea* was present in the Homestead Knoll area by 11,300 years B.P. and remained a common species in the small mammal fauna through much of the Early Holocene. After ca 8200 years B.P., however, *N. lepida* became the overwhelmingly dominant member of the genus, and *N. cinerea* became locally rare. Since mammals from later strata within Homestead Cave

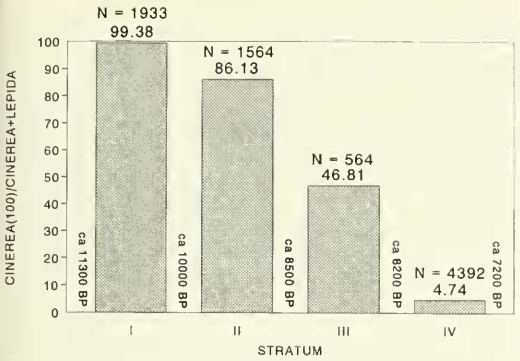

Fig. 3. Changing contribution of *N. cinerea* to the *Neotoma* (*N. cinerea* plus *N. lepida*) fauna, Homestead Cave strata I–IV (N = total number of *Neotoma* specimens identified to the species level, including those identified as *N.* cf. *cinerea* and *N.* cf. *lepida*).

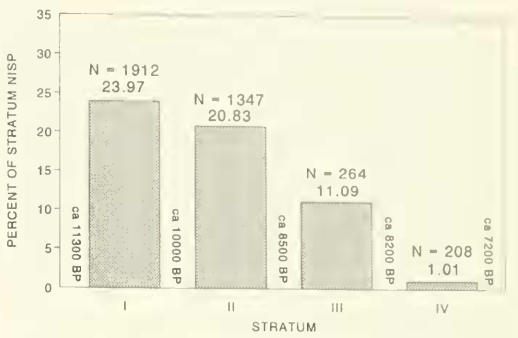

Fig. 4. Changing contribution of *Neotoma cinerea* to the total number of identified mammalian specimens (NISP) per stratum at Homestead Cave, strata I–IV.

have not yet been completely identified, we do not know whether *N. cinerea* survived the very xeric Middle Holocene (ca 7500–5000 years B.P.) here.

Currently, there are 2 options for explaining the modern existence of *N. cinerea* on Homestead Knoll. First, animals living here today may be direct descendants of the initial woodrat colonizers of the knoll, colonizers that arrived sometime between 14,500 and 11,300 years B.P. If so, the population has survived even though its numbers dropped precipitously toward the end of the Early Holocene (ca 8200–7200 years B.P.), and presumably fell even further during the heart of the Middle Holocene. Assuming that *N. cinerea* does not now survive in the valleys that separate Homestead Knoll from nearby uplands, and that it has not been able to survive in those valleys since at least 7000 years B.P., then this population has existed on an isolated upland a few thousand acres in extent for a minimum of some 7 millennia.

The other, and certainly more likely, option is that *Neotoma cinerea* has not been isolated on Homestead Knoll for this entire period of time, that populations on the knoll have been augmented by immigrants from elsewhere, and that any local extinctions of *N. cinerea* on the knoll have been followed by recolonizations from nearby populations. Indeed, it is even possible that the current representatives of the species colonized Homestead Knoll during the mid-1980s, a time of extraordinarily high precipitation in the northern Great Basin (Arnow and Stephens 1990).

IMPLICATIONS

The discovery of *Neotoma cinerea* on Homestead Knoll does not simply represent an unexpected natural historical tidbit. Our discovery documents either that populations of *Neotoma cinerea* within the Great Basin can find sufficient refuge in low-elevation, xeric habitats to survive for many thousands of years, or that this species can move across xeric lowlands far more readily than has been appreciated, or both. Indeed, insofar as bushy-tailed woodrats are more effective colonizers than has been realized, an effective parallel may exist in the yellow-nosed cotton rat (*Sigmodon ochrognathus*), a "montane" mammal of the Southwest that has apparently expanded its range across low-elevation valleys during the past 50 years (Davis and Dunford 1987; see also Davis and Callahan [1992] on *Microtus mexicanus*).

Elsewhere, Grayson and Livingston (1993) have noted that *Sylvilagus nuttallii* can cross valley bottoms in at least parts of the Great Basin. Now, it seems that *N. cinerea* can survive in habitats that are anything but montane. This fact leads us to suggest that the nestedness of Great Basin mammal faunas (sensu Patterson and Atmar 1986, Patterson 1987, 1990) might reflect a combination of extinction histories *and* colonization abilities. In addition, the Homestead Knoll record for *N. cinerea* takes its place alongside other recent data documenting that current models of Great Basin small mammal biogeography are far too static to encompass properly the wide range of geographical and biological variability that has produced the modern distribution of those

mammals that, for several decades, have been treated as "montane" within the Great Basin (e.g., Grayson 1993, Grayson and Livingston 1993, Lawlor 1995, Rickart 1995). In the Southwest, modern montane mammal distributions have clearly been determined by a complex combination of Holocene extinctions and colonizations (e.g., Davis and Dunford 1987, Lomolino et al. 1989, Davis and Callahan 1992). It now appears that the situation in the Great Basin is quite similar.

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